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ENERGY FLOW IN ECOSYSTEMS AND ITS EXPLOITATION BY GRAZING

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ABSTRACT

A brief discussion of the definition and measurement of energy flow in ecosystems is followed by an analysis of some known ecosystems. These are broken down into their trophic components. The relative magnitudes of respiration, yield to grazing, production of non-grazed organic matter by plants and of metabolic and growth efficiency by animals are compared over a range of contrasting systems including grassland and plankton. It is shown that the various routes of energy flow and the relationships between stock and productivity vary over several orders of magnitude depending on the biology of the organisms involved. This is reflected in the greatly different yields obtained by conventional grazing practices. The ecological framework within which it is possible to manipulate ecosystems for the purpose of increasing grazing yields is then defined and present performance is compared with the potential yields.

In this paper I shall attempt to deal with the factors which limit the productivity of ecological systems involving grazing. I must stress that my qualifications for tackling this task are meagre; my own research is hardly relevant to the ecology of grazing and I should be grateful if experts would correct any mis-statements I may make. It seemed useful at the outset, before treating the more specific aspects of the symposium, to look for the major factors which different grazing systems have in common, to compare the conclusions which have been reached in published work and to devise a scale by which estimates of grazing quantities for different systems can be compared. This is the more necessary because our topic is covered by many kinds of biologists who write in many different journals, and they do not all speak the same language. As a result, we find the situation, so familiar in ecology, in which a number of different terms are employed for the same concept whilst the same term is used by different authors to mean different things. A more elusive variant of the latter difficulty is the way in which concepts effectively change their meaning — or at least their significance — when transposed from one field to another on account of differences in the magnitude of the quantities involved. I propose to try to use a consistent set of words, but if in doing so I misinterpret their implications in a particular field I hope — and expect — that this will be clarified in discussion.

In outline, I propose to begin by considering in theory what happens to the solar energy which flows through a closed ecological system. Then I shall dismantle this theoretical system and, by means of figures from a range of published examples, I shall attempt to fit typical magnitudes to some of the component parts, and then reassemble the complete system and examine the effects of the idiosyncrasies of the parts on the structure of the whole.

Finally, I want to consider the boundaries which ecological theory would seem to impose on the returns which are to be obtained by manipulating ecological systems for human gain. I hope that you will not misunderstand me here; I realize that farming and other methods of food production are dominated by what is economically possible, but on this occasion I suggest that we concern ourselves with the wider range of what is ecologically possible because we are, after all, ecologists and therefore interested in generalizations about the structure of living systems. In a world which is getting hungrier today's impractical ideas have a way of becoming tomorrow's technical realities.

The first figure is a grossly oversimplified illustration of the pathways of energy through an ecosystem. In this I have made the following assumptions. First, that one can validly think of energy as flowing between organisms when in fact it takes the form of separate individual creatures and separate meals; secondly, that the system is isolated from all other systems; and thirdly, that organisms can clearly be separated into 'trophic levels' as plants, herbivores, carnivores and decomposers. The main points I want to illustrate are the differences between the schemes in relation to energy flow, to organic matter containing energy and to inorganic matter from which energy has been removed. If the system is assumed to be in a steady state, the quantity of solar energy taken up by photosynthesis is equal to the sum of energy losses derived from respiration of all the organisms, plant and animal, present. The metabolism of the plants is limited either by solar energy or by nutrients; if the non-photosynthetic components of the system were to break down the plants would be denied fresh supplies of nutrients and would eventually be unable to maintain active photosynthesis. From this point of view, given unlimited light, the more rapidly that organic foods are oxidized and their energy and nutrients are liberated the more rapid will be the rate of plant metabolism; any bottlenecks in the cycle of breakdown will reduce plant productivity.

Let us now examine in more detail what happens at the plant level. In Fig. 2, the area of the central rectangle represents the stock of organic material in the living plants. The flow channels from six o'clock to ten o'clock represent the flow of energy into and out of the system. The channel at twelve o'clock represents the output of organic matter as green food to herbivores and the channel at two o'clock the output as dead plant matter to decomposers. The arm at three o'clock represents the interchange of inorganic nutrients and carbon dioxide mostly into but partly out of the

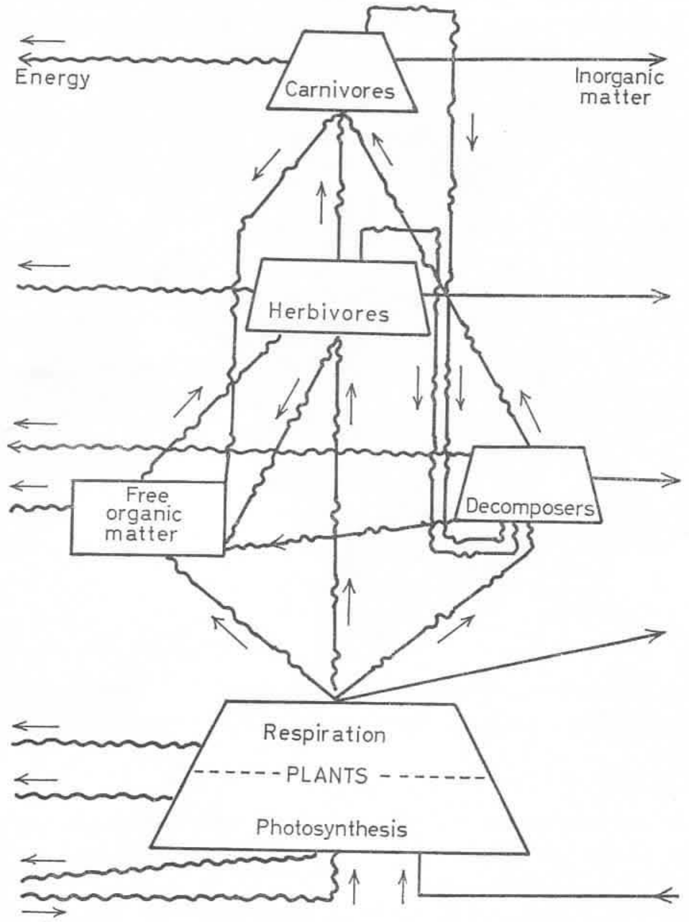

FIG. 1. Theoretical energy flow scheme in an isolated system. ∿∿∿∿ = paths of Energy; —∿—∿ = paths of organic matter; ——— = paths of inorganic matter.
Solar energy enters only from the bottom. Details see text.

plant stock. Since this cannot usually be analysed under natural conditions we shall omit it from later diagrams. The conventional positions occupied by each form of energy flow will be adhered to in describing six examples of primary production systems from nature, which are shown in Fig. 3.

A. A managed forest of *Picea omorika* in Britain described by Ovington and Heitkamp (1960). This is assumed to be cut down once every 21 years and to be provided with fresh supplies of fertilizer; it represents about the most productive primary system in the open in our climate. The stock is taken to be the average throughout the period of growth.

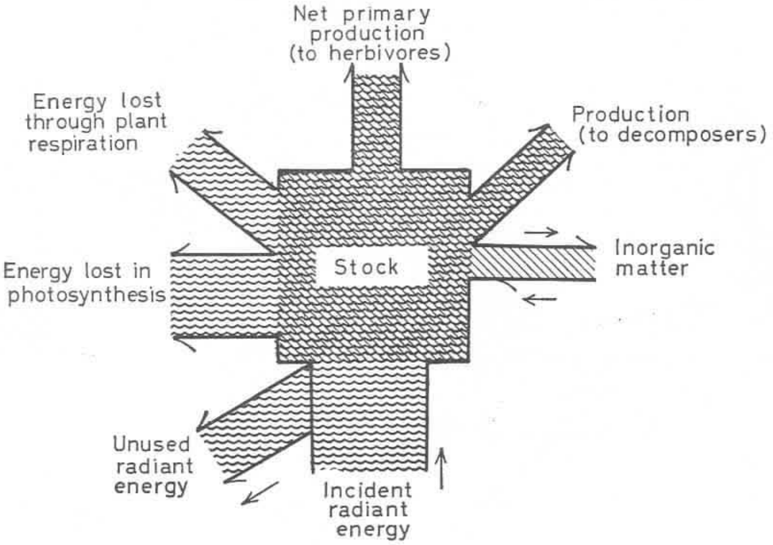
Net primary production (to herbivores)
Energy lost through plant respiration
Production (to decomposers)
Energy lost in photosynthesis
Stock
Inorganic matter
Unused radiant energy
Incident radiant energy

FIG. 2. Scheme for energy and matter flow through plant level. ≈≈≈≈ = energy paths; ▩ = paths of organic matter; \\\\\\\\\ = paths of inorganic matter.

B. A normal reasonably fertile grass field exploited by grazing under British conditions (data modified from Golley (1960), Stamp (1958), Odum (1959), Albriton (1953)).

C and *D*. Two examples from an unexploited salt marsh at Sapelo island described by Odum and his colleagues (Odum, 1960; Pomeroy, 1959; Teal, 1959; Smalley, 1960). Firstly (*C*) the food chain based on the algae which live on the mud (Pomeroy, 1959) and secondly (*D*), that supported by *Spartina* (Smalley, 1960).

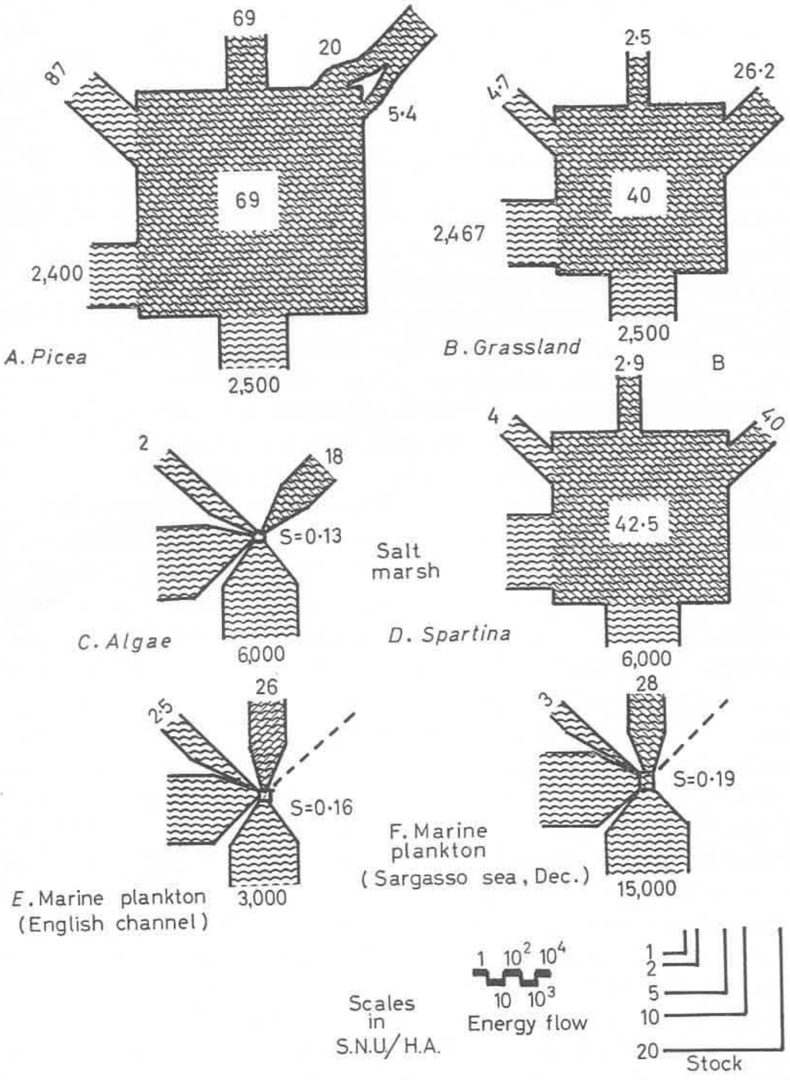

FIG. 3. Scaled flow paths for six actual plant systems. Mean stock is proportional to the area of the central square.
Flow channels are logarithmically proportional to mean annual energy flow. The units are S.N.U. (= 10^6 Calories) per hectare. Conventions as in Fig. 2.

E and *F*. Two examples of marine plankton communities discussed by Cushing (1955, 1959a, 1959b).

An appreciation of energy flow may be made difficult by unfamiliarity with the magnitude of the different units employed. I am therefore adopting the S.N.U. or Standard Nutritional Unit proposed by Stamp (1958) which has the advantages that it can usually be employed without using too many zeros or decimals and that it is the amount of energy which we ourselves consume in a year assuming a daily ration of 2,640 cal and a 10 per cent loss of calories in cooking. This unit is exactly a million large Calories. The unit of area is the Hectare (2·47 acres). If you are unfamiliar with hectares you can divide the figures given by 10 and think of them as applying to a quarter-acre vegetable garden. The time unit for flow is the year. Stock, of course, is not a rate of flow but a quantity of matter and the relation between the flow 'channels' and the stock 'boxes' is therefore arbitrary. Where possible I have used known calorific coefficients but where, as is usually the case, these are not known I have assumed that one gram dry-weight of organic matter has an energy content of four Calories; this is only one of the factors which make these calculations extremely rough. The flow scales in all these diagrams are logarithmic and the stock scales are proportionate in *area* to the logarithm of the caloric value of the stock.

The most interesting differences between these diagrams seem to me to be these. Firstly, the algae, as opposed to the higher plants, do comparable amounts of metabolic work with the aid of a very much smaller stock of material. This confirms expectations that metabolic rates per unit of mass increase with the surface-to-volume ratio (Zeuthen, 1947). Secondly, notice that by far the greater part of solar energy which is actually absorbed by the plant is lost through the relative inefficiency of photosynthesis. As a result there is little relation between yield to herbivores and incident solar radiation. This is something we cannot do very much about. Note, however, that losses are greater for grass and *Spartina* than for the *Picea* forest. Thirdly, of the energy which is incorporated in plant tissue a fairly constant amount is respired, again except in the case of the forest. Fourthly, from the plant's point of view as it were, what happens to the remainder of the energy going to herbivores and decomposers is not of great moment; but from the point of view of the whole system there is a very great difference between the 'productive' systems, such as the phytoplankton, of which nearly all is eaten by herbivores and a negligible quantity allowed to die 'naturally', and the grass of which by far the greater amount is never eaten during the growing season but goes to feed the decomposer industries. At this point, therefore, there is a major division in the energy flow scheme which decides whether a community shall contain a high or a low proportion of plant-derived dead organic matter on the one hand and a small or large herbivore industry on the other.

Presumably this reflects some special features of the biology of the higher land plants as compared with aquatic algae; perhaps their evolution of defence mechanisms such as silica spines on the edges of leaves ensures that they are not so readily eaten during life. At all events the result of this contrast is that most of the biomass of animals in most terrestrial habitats is to be found in decomposer organisms whilst there are very few of these in the plankton.

Notice too that the ratio of stock to herbivorous production varies enormously. In the case of the grasses, much plant material remains free from herbivore attack at the end of the season, whilst in the plankton the algae are grazed many times over. This means that turnover of nutrients is necessarily much slower in the former whilst in the latter the very growth of later generations of algae depends on their ancestors having been eaten and the nutrients released by zooplankton earlier in the year.

All this serves, of course, to underline the falsity of relying on stock figures as a guide to production rates. This point has been further clarified by Cushing (1959a, 1959b) in his comparison between temperate marine plankton and that in the Sargasso. The diagram shown here is for the peak season of activity in the winter and a similar diagram for summer would have shown a much smaller stock. In fact, there is remarkably little difference between the primary production picture for the Sargasso and for the English Channel, because in the Sargasso the much greater depth of planktonic activity and sunlight penetration compensates for a more dilute plankton.

Notice too, that the *Picea* forest is a managed system in which most of the production is removed as timber. Naturally, in an unexploited woodland, by far the greater part of the 69 S.N.U. yield would join the unexploited roots (20 S.N.U.) and the litter (5·4 S.N.U.) which at present go to the decomposer organisms.

In order to give scale to some typical man-managed systems I have given in Table 1 a few yield figures in S.N.U. Apart from the enormously greater yields obtainable under a tropical sun I think perhaps the most interesting points to observe here are firstly that intensive cultivation can produce comparable yields to natural systems depending on the trouble taken over the different methods of culture and secondly that the great increases due to fertilizer application indicate that nutrients and not solar energy are often the limiting factors in production.

TABLE I

Approximate net annual primary production from some man-managed systems

Vegetation	S.N.U./ Hectare	Source
Old Field Grass	3·2	Minnesota. Bray *et al.*, 1959
Maize unfertilized	8·2	
„ fertilized	24·4	
Typha	31·2	
British Farming		Stamp, 1958
Grazing (improved)	1·0	
National average	7·0	
Best	13·6	
Europe. Wheat max.	8·3	
Sugar beet	60·5	4 months only. Best Gaastra, 1958
Sugar mean	65·5	Odum, 1959
max.	254	
Cassava	280	Kalle, 1948
Algal culture	300	Fogg, 1958

The next figure (Fig. 4) is intended to show what happens to the food which is obtained by herbivores from plants. Much of the energy available in the form of plant matter is not, of course, grazed by economically favoured species because it is used by rival herbivores or because it is simply not available in the right form at the right time. Of the calorific value in food ingested a considerable proportion, varying usually from about 40 per cent to more than 90 per cent is rejected as faeces, only a reduced amount being actually assimilated. A proportion of the assimilated food is stored in the tissues of the animal or is used in the formation of eggs or young and thus contributes to the growth of the stock of the population. The rest of the food is broken down to produce excreted matter of reduced energy content and, at the same time, energy is liberated in the form of heat or mechanical work. This exploitation of the potential energy is an irreversible process which can only occur once in the ecosystem and this explains the value to the ecologist of respiration measurements as an index of ecological importance. The stock in turn is exploited by predators which therefore stand to benefit from a high secondary net production rate.

The ratios of energy flows at different stages represent efficiencies and a great many such ratios have been recognized according to the viewpoint of the investigator (see Slobodkin (1960) Pattern (1959)). For instance, the ecologist interested in the community as a whole is concerned with losses in energy content between equivalent stages in succeeding trophic levels and concentrates on the *ecological efficiency* E4/E1. (See Fig. 4.) The pig farmer who wants to obtain as much pig meat per unit of feeding stuff as possible can eliminate losses to rival herbivores provided he can control the depredations of rats and grain weevils. He can also avoid losses through disease which would feed the decomposers, but he must take into account the metabolic cost to the sow of producing piglets as well as the feeding cost of raising weaners. He is therefore concerned with what Slobodkin

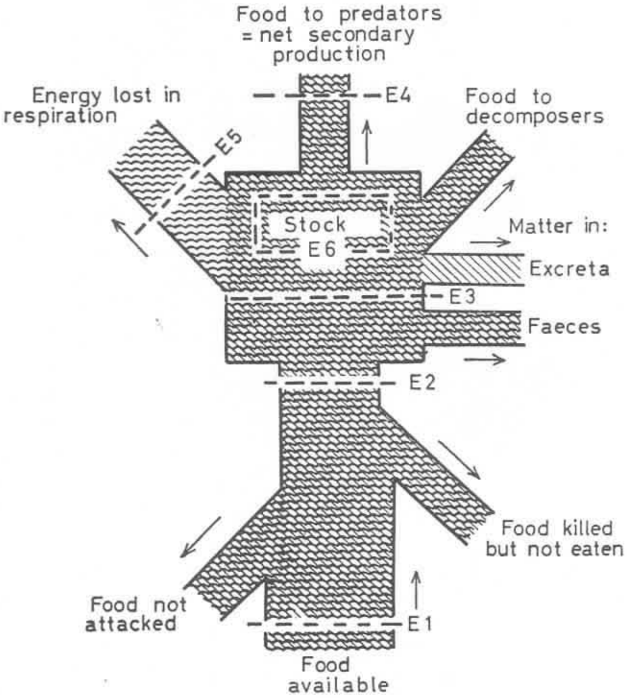

FIG. 4. Scheme for energy and matter flow through herbivore level. Conventions as in Fig. 2.
Ratios of the flows at points marked are efficiencies: E4/E1 = ecological efficiency; E6/E2 = growth efficiency when measured throughout development; E5/E3 = Teal's efficiency; E6/(E3–E5) = efficiency in the sense used by fisheries biologists.

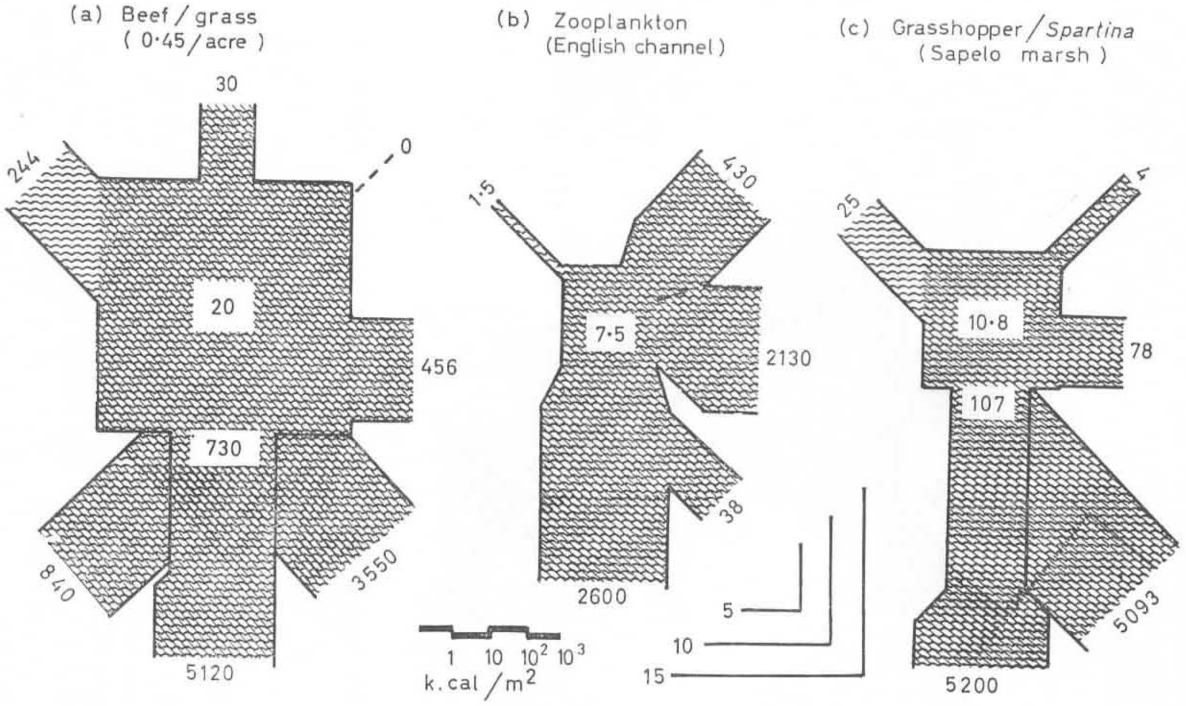

FIG. 5. Scaled flow paths for three herbivore systems. Conventions as in Fig. 4.

has defined as *growth efficiency*. Other measures of efficiency, each of which is perfectly logical and legitimate in its appropriate context, are indicated in the figure; I only want to stress at this stage that the undefined use of the term 'efficiency' by different groups of people has, in the past, lead to a good deal of confusion.

If we now examine some actual examples of energy flow through the herbivore levels of some of the communities we are studying (Fig. 5) we find that there are very great discrepancies even in the order of magnitude of the different flow paths. First, I should point out that the scales are about 100 times larger than those for primary production (Fig. 3) and that this is reflected by the use of a unit one hundredth of the S.N.U. per hectare, namely the Calorie per m^2. Secondly, it is important when considering grazing animals and their food to take account of the time factor. Most frequently the food organisms breed more rapidly than their consumers and this can result in apparently small stocks of food organisms supplying herbivores at a very rapid rate. This evidently happens in the case of the zooplankton as we shall see below, and is equally obvious in the case of carnivores grazing on herbivores. For instance Allen (1951) showed that the trout in the Horokiwi stream grazed the bottom living invertebrates to an extent of over forty times the maximum standing crop in the course of a year and Horton (1961) has since found a similar situation among trout in a Dartmoor stream. Thirdly, I have had to amalgamate the yields to herbivores and to decomposers in most cases because we do not know the proportions which go to each. As I said of the plant level, it is not of fundamental importance to the herbivores whether they succumb to predators or to disease; it is only the human predator who tries to maximize the first and minimize the latter and it is in this direction that man has a chance to switch the energy flow to his own advantage with least influence on the metabolism of the ecosystem as a whole. Thus the successful raiser of bullocks can hope for a maximum yield of 30 calories per square metre from an initial grass production of over 5,000. Notice (Fig. 5a) that the bullocks have selected only about one seventh of the available herbage in favour of other herbivores and decomposers, have rejected nearly two thirds of their food in faeces and have respired nearly 90 per cent of what they do assimilate. If he fails to keep his stock healthy much of the 30 calories of yield will go to feed the decomposers also.

The Sapelo marsh Grasshopper *Orchellimum fidicinium* (Fig. 5c) which was studied by Smalley (1960) seems fairly typical of most herbivorous insects in that feeding is very selective but the proportion of ingested food which is actually assimilated is fairly high — about 25 per cent. Also notice that a very high proportion of the assimilated food is respired again. This is a particularly characteristic feature of terrestrial arthropods and perhaps reflects the high metabolic demands of life on land. In the case of such an animal and for the purpose of comparing different species, the near equality between respiration and assimilation may make it permissible to measure whichever is more convenient, as Phillipson has done in his studies on the harvestman *Mitopus morio* (1960a, 1960b). In the case of fishes, on the other hand, which lay down as body flesh a higher proportion of their food, this is often not legitimate.

The third part of this diagram (Fig. 5b) represents the English Channel zooplankton. It is rather badly distorted by the fact that values are averaged over the year although in fact most of the activity is confined to three or four months in the summer. It will be remembered that they press so closely on the heels of the phytoplankton that very little of the latter remains un-eaten. However, as Cushing has shown (1959a, 1959b) the free organic matter in the sea is derived largely from a different source, namely the fact that copepods, when food is abundant, become fantastically inefficient feeders and defecate five and even ten times as much plant food as is required for metabolism. This has important consequences for the community as a whole, it accelerates the liberation of nutrients to plants and to some extent it provides a reserve of food for the long period between summer plankton blooms, but in the present context it results in the copepods liberating the energy from only a small proportion of the food available to them and thus contributing enormously to the free organic matter of the sea. The story of the marine zooplankton is far from unique. Slobodkin found the same overfeeding phenomenon in his culture experiments with *Daphnia* (1954), Gajevskaya (1959) found that marine Isopods fed wastefully on higher plants in the Black Sea and a number of authors have detected similar behaviour among land arthropods such as Diplopods (Dunger, 1960). In each case we have an important diversion of organic matter, usually readily accessible to microbial attack, from the herbivorous food chains.

Before material is attacked by the decomposers it is present in the form of undecomposed organic matter, a feature of most natural systems which we are inclined to overlook. However, according to Fogg (1959) the quantities of dissolved organic matter present in lake waters may be from six to four thousand times that in particulate form. Again, soils of the möder type are known which almost entirely consist of the faeces of arthropods (Kubiena, 1953). Fox (1955) has estimated a free organic content of the world's oceans about fifty times as great as the annual photosynthesis. This, of course, implies a very slow rate of turnover but the significant point in the present context is the existence of vast reserves of nutrients and energy locked up and only slowly being exploited.

Some of the organic material is known to be oxidized directly; this happens to copepod faeces in tropical seas (Cushing, 1959b) and also under high temperature conditions in desert soils (Bunt *et al.*, 1954). Direct chemical oxidation is presumably a useful supplement to biological breakdown, provided it does not imply loss of nitrogen and soluble salts nor unfavourable physical changes in the medium, as happens when vegetation is burned. The relative importance of direct oxidation is not yet clear but it seems to be appreciable in some conditions in warm climates.

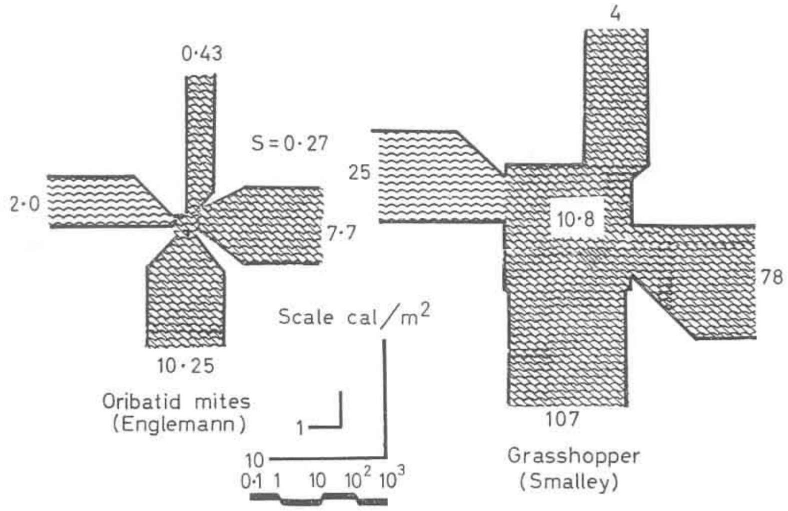

FIG. 6. Scaled flow paths comparing a decomposer with a herbivore system (Oribatid mite population after Englemann, 1961 and Grasshopper population after Smalley, 1960).

This leads to a brief consideration of the organisms which are responsible for the breakdown of most of the free organic matter in all its forms. A full treatment of this subject would be a lengthy matter, especially in the case of terrestrial environments, such as grassland, where by far the greater part of both species and biomass are involved in this decomposer industry. From the present point of view, however, I want first to point out that a great many organisms are involved and that organic matter is subjected to a whole succession of processes, such as concentration, comminution, mixing with mineral matter and changes in physical structure by animals as diverse as filter feeders, millipedes, earthworms and fiddler crabs.

I have one figure (Fig. 6) which allows us to compare the flow sheet for the grasshopper *Orchellimum* with Englemann's (1961) field results from a small arthropod decomposer population in a meadow. The main feature to notice is that the detritus feeding Oribatid mites, as we might expect, seem able to process proportionately more material and energy with much less biomass than the herbivore. It is my guess that this is a valid generalization and my conviction, based on knowledge of metabolic activity, that a similar comparison of Collembola with *Orchellimum* would show an even greater discrepancy. On the whole detritus feeders abstract rather little energy in proportion to the material they handle but the effects of their activities are important because the material is usually made more accessible to attack by bacteria and fungi especially when, as in the case of soil, it is both moistened and aerated. We have also recently become aware (Van der Drift, 1959 ; Witkamp, 1960; Macfadyen, 1961) that the effects of such detritus feeders are out of all proportion to their own metabolic activities because, by spreading of spores, by breaking down microbial antagonisms and in other ways, they greatly accelerate the activities of the microorganisms.

Next I should like to consider what happens when we re-synthesize something like a complete ecosystem from its components. Fig. 7 is the scaled version of my first diagram on the basis of some figures from grassland. Apart from the points I raised before about photosynthetic inefficiency and energy loss from beef as faeces, the outstanding feature must surely be the enormous accumulation of organic matter in the soil, mostly at the surface. The greater part of this comes from the grass but an appreciable quantity exists in the form of cow pats. The stock of decomposer organisms as a whole contains about the same quantity of energy as the grass but compared to the cattle and to other herbivores it is slow in processing the organic material which is its food. It seems clear from other analyses (Macfadyen, 1961) that the animals in soil and litter contribute barely 10 per cent to the total metabolism of the decomposers, the remainder being carried out by microorganisms. For the reasons mentioned above, however, this does not imply that removal of the animals would decrease the energy flow and nutrient liberation from the organic matter by only 10 per cent. Indeed, to judge from what happens in acid mor conditions or when animals are suppressed by toxic chemicals it is clear that when all decomposition is left to the microorganisms, organic matter usually accumulates from year to year. The decomposer industry is clearly a complex one

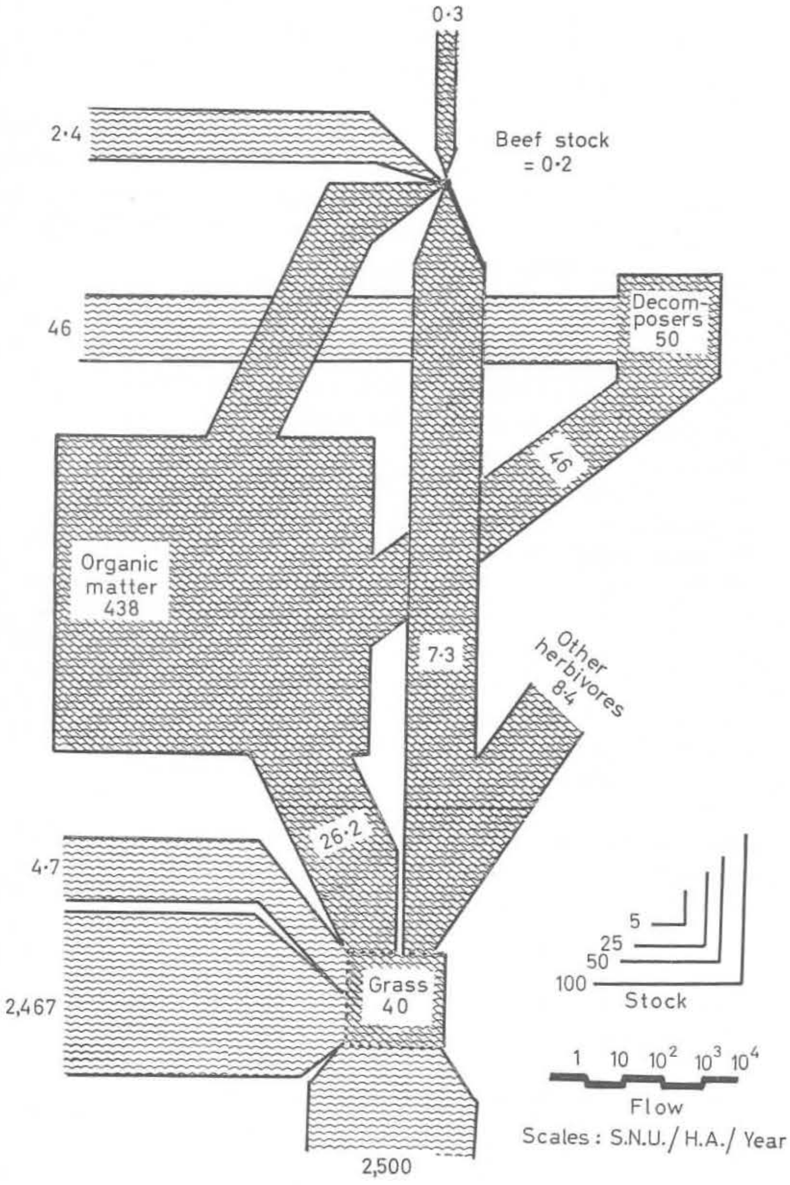

FIG. 7. Scaled version of Fig. 1 with values obtained from meadow subject to grazing by beef cattle.

involving many different stages and subject to dislocation in many different ways. In the case of the permanent grassland shown in Fig. 7, it is clearly the activity of the decomposers which limits the productivity of the whole system, grazing included.

I have not the data to construct a similar scheme for the salt marsh and the marine plankton, but in both these systems we have noticed that a high proportion of the plant production appears in the form of accumulation of organic matter and it seems most likely that here too the decomposer organisms limit the overall turnover.

This survey of the ecological potentialities of a highly theoretical scheme does not, of course, give the ecologist the right to tell practical people how to conduct the detailed management of living systems. It does, though, indicate some possible ways in which they might consider diverting organic production for human use. We know, from experience with terrestrial systems that we can profitably supplement or substitute chemically derived nutrients for those which a too slothful soil community is failing to supply. There was a period when similar fertilization was advocated as a stimulus to marine systems, but it now seems that a more profound knowledge of the rather lengthy food chains is required. In principle there are likely to be more losses in such a system between photosynthetic and predatory fish production than between the farmer's pasture and arable crops and agricultural food products. In the case of already fertile systems such as salt marshes, Odum's (1960) suggestion that the exploitation of detritus feeding molluscs and crustacea should take precedence over attempts to harness a not very prolific herbivore chain deserves careful consideration.

This raises the further point, which I have omitted hitherto for the sake of simplicity, that calorific content is far from being the only criterion of a satisfactory human diet. The crops which produce the highest calorific yield for instance, are those which are most deficient in proteins. It is now generally accepted that the human diet requires about 20 gm of protein per 1,000 Calories. Clearly at the present time there is much to be said for encouraging the production of animal food, especially where this can be done by using detritus feeding animals and with relatively little expense. The relative economic advantages of more ambitious schemes both for cereal production and for protein production by unconventional methods, such as Pirie (1958) has advocated, are matters of economics and human need which must be weighed by others; the ecologist can only indicate new fields which seem to have been overlooked and the rules within which human endeavour must operate.

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